

Scotland's Rural College

## **Heterosis in cattle crossbreeding schemes in tropical regions: meta-analysis of effects of breed combination, trait type, and climate on level of heterosis**

Bunning, Harriet; Wall, E; Chagunda, MGG; Banos, G; Simm, G

*Published in:*  
Journal of Animal Science

*DOI:*  
[10.1093/jas/sky406](https://doi.org/10.1093/jas/sky406)

First published: 20/10/2018

*Document Version*  
Peer reviewed version

[Link to publication](#)

### *Citation for pulished version (APA):*

Bunning, H., Wall, E., Chagunda, MGG., Banos, G., & Simm, G. (2018). Heterosis in cattle crossbreeding schemes in tropical regions: meta-analysis of effects of breed combination, trait type, and climate on level of heterosis. *Journal of Animal Science*, 97(1), 29-34. <https://doi.org/10.1093/jas/sky406>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

# Heterosis in cattle crossbreeding schemes in tropical regions: meta-analysis of effects of breed combination, trait type, and climate on level of heterosis<sup>1</sup>

Harriet Bunning,<sup>\*,†</sup> Eileen Wall,<sup>\*</sup> Mizeck G. G. Chagunda,<sup>‡</sup> Georgios Banos,<sup>\*,‡</sup> and Geoff Simm<sup>†</sup>

<sup>\*</sup>Animal & Veterinary Sciences, Scotland's Rural College, King's Buildings, West Mains Road, Edinburgh EH9 3JG, UK

<sup>†</sup>Global Academy of Agriculture and Food Security, University of Edinburgh, Edinburgh EH25 9RG, UK <sup>‡</sup>Department

of Animal Breeding and Husbandry in the Tropics and Subtropics, University of Hohenheim, 70599 Stuttgart, Germany

<sup>†</sup>The Roslin Institute, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Edinburgh EH25 9RG, UK

**ABSTRACT:** The aim of this study was to investigate the effects of animal trait, breed combination, and climate on the expressed levels of heterosis in crossbreeding schemes using tropical cattle. A meta-analysis of 42 studies was carried out with 518 heterosis estimates. In total, 62.5% of estimates were found to be significantly different from zero, the majority of which (89.8%) were beneficial for the studied trait. Trait and breed combination were shown to have a significant effect on the size of heterosis ( $P < 0.001$  and  $P = 0.044$ , respectively). However, climate did not have a significant effect. Health, longevity, and milk production traits showed the highest

heterosis ( $31.84 \pm 10.73\%$ ,  $35.13 \pm 14.35\%$ , and  $35.15 \pm 3.29\%$ , respectively), whereas fertility, growth, and maternal traits showed moderate heterosis ( $12.02 \pm 4.10\%$ ,  $12.25 \pm 2.69\%$ , and  $15.69 \pm 3.26\%$ , respectively). Crosses between breeds from different types showed moderate to high heterosis ranging from  $9.95 \pm 4.53\%$  to  $19.53 \pm 3.62\%$ , whereas crosses between breeds from the same type did not express heterosis that was significantly different from zero. These results show that heterosis has significant and favorable impact on productivity of cattle farming in tropical production systems, particularly in terms of fitness but also milk production traits.

**Key words:** crossbreeding, heterosis, meta-analysis, tropical cattle

© The Author(s) 2018. Published by Oxford University Press on behalf of the American Society of Animal Science.

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)

J. Anim. Sci. 2018.XX:XX–XX  
doi: 10.1093/jas/sky406

## INTRODUCTION

Heterosis is the difference in phenotype between the mean of crossbreds and their purebred parents (Notter et al., 2013). In animal breeding, this is usually expressed as mid-parent heterosis or the superiority of the F1 cross over the mean performance of the 2 parents (Dickerson,

1969, 1973) and has been shown to occur across species (reviewed in: Sheridan, 1981). Deviations from the mid-parent value can be positive or negative but are mostly found to be beneficial (Powers, 1944). In cattle breeding, crossing has been used to take advantage of heterosis under a range of systems. In temperate systems, heterosis has been shown for fertility (Coffey et al., 2016), milk (Lembeye et al., 2016), and growth traits (Schiermister et al., 2015). In the tropics, a variety of crossing strategies have been implemented with varying levels of success (reviewed in: McDowell, 1985; Cunningham and Syrstad, 1987).

<sup>1</sup>H. Bunning would like to thank SRUC for funding her PhD.

<sup>2</sup>Corresponding author: [harriet.bunning@sruc.ac.uk](mailto:harriet.bunning@sruc.ac.uk)

Received July 16, 2018.

Accepted October 15, 2018.

The performance of these crosses is dependent on the expression of additive and nonadditive genetic effects, particularly heterosis. To design an effective crossing strategy, it is important to understand how heterosis varies across different traits, depending on breed combination and environmental conditions, particularly in tropical systems with diverse breeds and environments. Meta-analyses are useful in aggregating results from a variety of studies and quantifying the effect of specific factors. In previous reviews without meta-analysis, the effects of specific factors were not able to be quantified and a limited combination of breeds and traits tended to be investigated (Syrstad, 1985). In the current study, we quantify the benefits of heterosis across studies and identify factors influencing heterosis, including the breed combination, trait type, and climate. We also test heterosis globally to ensure results are not simply the effect of a specific set of experimental conditions, allowing more reliable parameter estimates for modeling (Sauvant et al., 2008).

## MATERIALS AND METHODS

### Literature Search

Crossbreeding studies which estimated heterosis effects were found from a literature search using Web of Science (ISI). The keywords heterosis AND cattle AND (“zebu” OR “sanga” OR “criollo” OR “indicus” OR “brahman”) were used and reference lists of the obtained articles were screened to find additional relevant papers, particularly those cited in key review papers (Mcdowell, 1985; Syrstad, 1985). A total of 134 articles were identified and screened. Articles were excluded if they did not include at least one tropically adapted breed and did not contain the required data for analyses, including standard errors. After editing, 42 studies (Supplementary Appendix Table 1) with 518 estimates were found to meet the criteria set and were retained for subsequent analysis.

### Data Extraction

The majority of studies contained multiple heterosis estimates for a variety of traits, breed combinations, and environments. For each heterosis estimate, the following values were recorded: the size of the effect, the standard error of the heterosis estimate, and the mean performance of the purebred. In studies where the average parental purebred performance was not recorded, it was calculated from the reported means for each purebred.

In addition, the breed combination, trait, and location of study for each heterosis estimate were recorded in order to define the type of cross, trait, and climate, respectively. Breeds were sorted into the following 3 types: European *Bos taurus* (E), tropical *B. taurus* (T), and tropical *Bos indicus*, also known as zebu (Z) (Supplementary Appendix Table 2). There were 6 possible pairs of parental breeds (including crosses within and across types); however, no studies were found of crosses between 2 tropical *B. indicus* type breeds, meaning there were a total of 5 cross type categories: European *B. taurus* × European *B. taurus* (ExE), *B. indicus* × *B. indicus* (ZxZ), tropical *B. taurus* × European *B. taurus* (TxE), tropical *B. taurus* × *B. indicus* (TxZ), and *B. indicus* × European *B. taurus* (ZxE). Traits were sorted into 11 types, including efficiency, fertility, growth, health, longevity, maternal, meat, milk, temperament, birth weight, and other (Supplementary Appendix Table 3). The location of the animals of the study was used to define the climate using the “Livestock Geo-Wiki” (Robinson et al., 2014), based on Robinson et al. (2011), as either arid and semiarid tropics and subtropics, humid and subhumid tropics and subtropics, or temperate and tropical highlands.

### Statistical Analysis

In order to standardize heterosis values from different studies and traits, these were expressed as a percentage of the mean performance of the 2 purebreds. Each estimate was multiplied by either 1 or −1, such that estimates in the desired direction for the trait were expressed as positive. The resulting values were used as the dependent variable in the model.

Following the guidelines for meta-analyses (Sauvant et al., 2008), each data point requires a measure of its reliability which is then used to weight it in the model. The standard error of an estimate is commonly used. However, in the present study, the units of standard errors vary due to multiple traits being tested. In order to standardize our standard errors, we divided each by the original heterosis estimate to remove the units. The inverse of this standardized standard error was then used as weight in the analysis, meaning that estimates with large standard errors contributed less to the result. All weights were made positive and to avoid using weights of zero, where the mean heterosis was equal to zero the weight was made equal to 0.0001.

The following model was used to assess the impact of the 3 factors on heterosis:

$$Y_{ijk} = \mu + T_i + B_j + C_k + e_{ijk},$$

where  $Y_{ijk}$  was the standardized heterosis for a trait type  $i$  ( $i = 1-11$ ), between breed cross type  $j$  ( $j = 1-5$ ) and in climate  $k$  ( $k = 1-3$ ). Trait type,  $T$ , cross type,  $B$ , and climate,  $C$ , were fixed effects and  $e$  was the random error term. For simplicity, the weights are not shown but, as stated previously, each value of  $Y$  was weighted according to the inverse of the standardized standard error.

## RESULTS

The mean heterosis was 12.9% (median = 9.4%) with an SD of 20.0%. Estimates ranged from -33.3 to 155.6%; among all estimates, 62.5% were found to be significantly different from zero (95% confidence interval). The majority of these showed beneficial heterosis but 6.4% of all estimates showed significant nonbeneficial heterosis. Trait type and cross type were shown to have a significant effect on the size of heterosis ( $P < 0.001$  and  $P = 0.044$ , respectively). However, climate did not have a significant effect.

Health, longevity, and milk production traits showed the highest heterosis manifested by the largest least squares means, although the standard errors of estimates for health and longevity were also large (LSM =  $31.84 \pm 10.73\%$ , LSM =  $35.13 \pm 14.35\%$ , and  $35.15 \pm 3.29\%$ , respectively). Fertility, growth, and maternal traits showed moderate heterosis (LSM =  $12.02 \pm 4.10\%$ ,  $12.25 \pm 2.69\%$ , and  $15.69 \pm 3.26\%$ , respectively). The LSM heterosis of all other trait types was not significantly different from zero (95% confidence interval) (Table 1).

**Table 1.** Least squares means and standard error of heterosis estimates (%) for trait type effect

Trait type	$N^1$	Least squares mean <sup>2</sup>	SE
Birth weight	72	-0.42 <sup>a</sup>	3.12
Efficiency	3	0.96 <sup>abc</sup>	19.00
Meat	48	6.07 <sup>ab</sup>	4.17
Temperament	2	-18.82 <sup>ab</sup>	13.22
Other	9	1.33 <sup>ab</sup>	10.25
Fertility	40	12.02 <sup>ab</sup>	4.10
Growth	185	12.25 <sup>b</sup>	2.69
Maternal	62	15.69 <sup>b</sup>	3.26
Health	6	31.84 <sup>abc</sup>	10.73
Longevity	2	35.13 <sup>abc</sup>	14.35
Milk	89	35.15 <sup>c</sup>	3.29

<sup>1</sup>Number of heterosis estimates for each level of the type trait effect.

<sup>2</sup>Means without the same superscript letter differ significantly,  $P < 0.05$

Crosses between tropically adapted *B. taurus* and temperate *B. taurus* breeds (TxEx) showed the greatest heterosis (LSM =  $19.53 \pm 3.62\%$ ) and crosses between zebu cross temperate *B. taurus* breeds (ZxEx) showed intermediate heterosis (LSM =  $15.04 \pm 2.92\%$ ). Crosses between tropically adapted *B. taurus* and zebu breeds (TxZ) showed the lowest heterosis of a between type cross (LSM =  $9.95 \pm 4.53\%$ ). The LSM of both within breed type crosses were not significantly different from zero (ExEx =  $8.22 \pm 4.63\%$  and ZxZ =  $6.88 \pm 10.81\%$ ) (Table 2).

## DISCUSSION

### Traits

Our results showed that health and longevity traits tended to show high heterosis, whereas in meat traits much less heterosis was expressed. This supports the view that traits that are more closely related to evolutionary fitness show greater heterosis (Merilä and Sheldon, 1999), as health and longevity are more directly related to fitness than meat type traits. It is suggested that traits with lower heritability, such as fitness traits, may have higher heterosis effects as they are largely affected by dominance (Merilä and Sheldon, 1999). This pattern was also found in a crossbreeding study of sorghum plants, where traits showing low heritability, such as grain yield, tended to have higher heterosis compared with more heritable traits, such as plant height (Liang et al., 1972). Similarly, results of a meta-analysis of inbreeding depression in 6 livestock species found meat and temperament traits did not show significant inbreeding depression, whereas adult survival and fecundity did (Leroy, 2014).

**Table 2.** Least squares means and standard error of heterosis estimates (%) for breed combination effect

Breed type <sup>1</sup>	$N^2$	Least squares mean <sup>3</sup>	SE
ExEx	65	8.22 <sup>a</sup>	4.64
TxE	80	19.53 <sup>a</sup>	3.62
TxZ	23	9.95 <sup>a</sup>	4.53
ZxE	332	15.04 <sup>a</sup>	2.92
ZxZ	18	6.88 <sup>a</sup>	10.81

<sup>1</sup>European *Bos taurus* × European *B. taurus* (ExEx), tropical *B. taurus* × European *B. taurus* (TxEx), tropical *B. taurus* × *B. indicus* (TxZ), *B. indicus* × European *B. taurus* (ZxE) and *Bos indicus* × *B. indicus* (ZxZ).

<sup>2</sup>Number of heterosis estimates for each level of the breed type effect.

<sup>3</sup>Means without the same superscript letter differ significantly,  $P < 0.05$ .



We might expect milk production traits to behave similarly to other production traits, such as growth or meat traits, but our results show these milk traits tend to also show high heterosis, similar to that expressed in health and longevity traits. There may be a number of reasons for this. First, we might consider milk production to be a fitness trait as it has an important effect on the survival of offspring. Therefore, we might expect it to have high heterosis, as for health and longevity traits. Also, we expect fitness traits to show higher heterosis because they have been under long-term, intense, directional natural selection (Merilä and Sheldon, 1999). In dairy cattle milk production, traits have also experienced very intense directional selection. Studies of European cattle genotypes show evidence for selective sweeps where strong selection for a trait has resulted in all genes in a region having gone to fixation, particularly in regions we now know contain genes with a strong influence on milk production (Hayes et al., 2009). We might expect milk production traits to behave similarly to fitness traits as both have experienced this intense directional selection. In a meta-analysis, Leroy (2014) found that across livestock species, some production traits tended to show high levels of inbreeding depression, particularly milk production which is in line with our results, but also litter weight, which while less important in cattle, where litter size is usually one, may also have been under strong selection in other species, particularly pigs (Groenen, 2016). However, in the study of Leroy (2014), birth weight was significantly affected by inbreeding depression, whereas we did not find any significant heterosis associated with birth weight. This may be due to the difference between species considered, especially since species such as pigs have large litters.

### **Breed Combination**

It is thought that genetic distance between parental breeds is very likely to have an effect on heterosis. One hypothesis is that increasing the genetic distance between breeds will increase the level of heterosis in their crosses. This can be explained by considering heterosis as the inverse of inbreeding depression, which occurs when 2 closely related individuals tend to have less fit offspring (Charlesworth and Charlesworth, 1987). The more distantly related parents are, the smaller the size of the inbreeding depression (Walling et al., 2011) which we could consider as an increased effect of heterosis. In a study of heterosis in protein

production in yeasts, Blein-Nicolas et al. (2015) found that interspecies crosses (crosses with more genetically diverse parents) tended to show more positive heterosis (78.8%) than intraspecies crosses (crosses with more closely related parents) (42.6 to 52.3%). A previous study of crosses of European dairy cattle breeds found increased heterosis in crosses where parental breeds are more distantly related (Gram and Pirchner, 2009) and this idea has been used in the past to predict heterosis using the genetic distance (Roughsedge et al., 2001).

Tropically adapted cattle breeds are more distantly related than any of the breeds measured in previous cattle studies. In some cases, crosses of very distantly related strains can lead to outbreeding depression, where heterosis effects are negative (Lynch, 1991). An extreme example of this is crosses between 2 different species where offspring are often infertile (for example, Ålund et al., 2013).

If heterosis in tropical cattle breeding is occurring as the inverse of inbreeding depression, we expect crosses between more distantly related breeds (TxE, ZxE, and TxZ in the present study) to show more favorable heterosis than crosses between breeds of the same type (ZxZ and ExE). Conversely, if outbreeding depression is occurring, we expect crosses between different breed types (TxE, ZxE, and TxZ) to show less favorable heterosis than crosses between breeds of the same type (ZxZ and ExE). Heterosis between distantly related breeds may even be negative; meaning the performance of the F1 is less favorable than the mean parental performance. Our results support the first hypothesis than heterosis is the inverse of inbreeding depression as the heterosis in ExE and ZxZ crosses was found to be less favorable than that expressed by TxE, ZxE, and TxZ crosses and the LS mean heterosis for all cross types was positive.

We can further group the 3 breed types in 2 different ways. Either according to subspecies type (*indicus* or *taurus*) or according to the climate for which they are adapted (temperate or tropical). If subspecies were more important, we might expect crosses between breeds from the same subspecies (TxE) to show lower heterosis than breeds from different subspecies (ZxE and TxZ). If climate adaptation were more important, we would expect crosses between breeds from the same climate (TxZ) to show lower heterosis than breeds from different climates (ZxE and TxE). Our results show that the lower heterosis for crosses between breed types was found in TxZ crosses, suggesting that diversity in climate adaption may be a better indicator for expected heterosis than the subspecies classification. This may also suggest

that tropically adapted taurine and zebu breeds are more closely related genetically than their classification might suggest.

There was large variation in the size of heterosis found in ZxZ crosses. This may suggest there is larger genetic diversity within this breed type as some crosses between closely related breeds expressed low levels of heterosis whereas others may be between more distantly related breeds and so express levels of heterosis closer to those found in crosses between different breed types. This is supported by a study of diversity of European and African cattle breeds, where although the average genetic distance between breeds from within each continent was similar (a mean Nei's genetic distance of 0.045 and 0.047 for breeds from Africa and Europe, respectively), the variation in genetic distance between breeds from Africa was larger than between breeds from Europe (an SD of Nei's genetic distances of 0.029 and 0.013 for breeds from Africa and Europe, respectively) (Gautier et al., 2007).

### Climate

Generally, more extreme climates are thought to lead to more extreme heterosis effects (Einfeldt et al., 2005; Penasa et al., 2010), potentially due to the increased importance of fitness traits in these environments. This is supported by a study that found inbreeding depression was greater in mice in the wild, compared to those kept in the lab where conditions were likely to be optimized (Jimenez et al., 1994). Tropical or arid environments may increase stress as cattle are more likely to experience heat stress, reduced food and water availability and therefore we might expect heterosis to be greater than that found in temperate climate. However, we did not find a significant effect of climate on heterosis in the present study.

Our climate measure may not be a good proxy for stress in cattle, as the majority of studies were conducted on research stations (39 out of 43), where we would expect conditions to be generally good, even under a harsher climate. There is also likely to be large variation in environment quality within each climate and this could explain why no effect of climate was found. Barlow (1981) carried out a review of heterosis  $\times$  environment interactions and found many studies across a wide range of species where the expression of heterosis varied across different environments. In general, a poorer environment led to greater heterosis, except in the case of growth and fecundity traits where this pattern was less clear. However, the authors also found problems with carrying out a strict meta-analysis

due to variation in environment conditions across studies and results are instead simply displayed as subjective tabulation.

Within a number of the studies included in our analyses, multiple environments were tested. In one study of Angus Brahman crosses, heterosis in a range of maternal traits was found to be greater when animals had poorer quality grazing (Brown et al., 1997). Similar results were found for milk production and somatic cell count (Brown et al., 2001). However, no differences were found between grazing type for heterosis in a range of growth traits (Brown et al., 1993).

### CONCLUSION

Results from the present study show that the type of trait and the combination of breed types both have a significant effect on the expression of heterosis. Heterosis was found to be beneficial for a range of economically important traits, including those related to fitness such as fertility and longevity, which are particularly important in low input systems common in the tropics. The most beneficial heterosis was found for milk production traits which are useful to farmers as it is directly linked to income. Crosses of breeds of different types expressed greater beneficial heterosis than those of breeds of the same type. The greatest heterosis was expressed in crosses of breeds adapted to different environments, rather than crosses of breeds which have been considered to be from different subspecies. These crosses of breeds adapted to different environments dominate in the tropics as they allow the combination of complementary production and fitness traits, meaning that there is great potential to utilize heterosis to increase profitability. Outcomes of the present study highlight and quantify the benefits of heterosis in crossbreeding as a tool to improve profitability of cattle farming in the tropics.

### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Animal Science* online.

*Conflict of interest statement.* None declared.

### LITERATURE CITED

- Ålund, M., S. Immler, A. M. Rice, and A. Qvarnström. 2013. Low fertility of wild hybrid male flycatchers despite recent divergence. *Biol. Lett.* 9:20130169. doi:10.1098/rsbl.2013.0169
- Barlow, R. 1981. Experimental evidence for interaction between heterosis and environment in animals. *Anim. Breed. Abstr.* 49:715–737.
- Blein-Nicolas, M., W. Albertin, T. da Silva, B. Valot, T. Balliau, I. Masneuf-Pomarède, M. Bely, P. Marullo, D. Sicard,

- C. Dillmann, et al. 2015. A systems approach to elucidate heterosis of protein abundances in yeast. *Mol. Cell. Proteomics*. 14:2056–2071. doi:10.1074/mcp.M115.048058
- Brown, M. A., A. H. Brown, Jr, W. G. Jackson, and J. R. Miesner. 1997. Genotype x environment interactions in Angus, Brahman, and reciprocal cross cows and their calves grazing common bermudagrass and endophyte-infected tall fescue pastures. *J. Anim. Sci.* 75:920–925. doi:10.2527/1997.754920x.
- Brown, M. A., A. H. Brown, Jr, W. G. Jackson, and J. R. Miesner. 2001. Genotype x environment interactions in milk yield and quality in Angus, Brahman, and reciprocal-cross cows on different forage systems. *J. Anim. Sci.* 79:1643–1649. doi:10.2527/2001.7971643x
- Brown, M. A., L. M. Tharel, A. H. Brown, Jr, W. G. Jackson, and J. R. Miesner. 1993. Genotype x environment interactions in preweaning traits of purebred and reciprocal cross Angus and Brahman calves on common bermudagrass and endophyte-infected tall fescue pastures. *J. Anim. Sci.* 71:326–333. doi:10.2527/1993.712326x
- Charlesworth, D., and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* 18:237–268. doi:10.1146/annurev.es.18.110187.001321
- Coffey, E. L., B. Horan, R. D. Evans, and D. P. Berry. 2016. Milk production and fertility performance of Holstein, Friesian, and Jersey purebred cows and their respective crosses in seasonal-calving commercial farms. *J. Dairy Sci.* 99:5681–5689. doi:10.3168/jds.2015-10530
- Cunningham, E. P., and O. Syrstad. 1987. Crossbreeding *Bos indicus* and *Bos taurus* for milk production in the tropics. FAO, Rome, Italy.
- Dickerson, G. E. 1969. Experimental approaches in utilising breed resources. *Anim. Breed. Abstr.* 37:191–202.
- Dickerson, G. E. 1973. Inbreeding and heterosis in animals. L. V. Cundiff, editor. *J. Anim. Sci.* 1973:54–77. doi:10.1093/ansci/1973.Symposium.54
- Einfeldt, C. H. P., S. Ceccarelli, S. Grando, A. Gland-Zwerger, and H. H. Geiger. 2005. Heterosis and mixing effects in barley under drought stress. *Plant Breed.* 124:350–355. doi:10.1111/j.1439-0523.2005.01111.x
- Gautier, M., T. Faraut, K. Moazami-Goudarzi, V. Navratil, M. Foglio, C. Grohs, A. Boland, J. G. Garnier, D. Boichard, G. M. Lathrop, et al. 2007. Genetic and haplotypic structure in 14 European and African cattle breeds. *Genetics*. 177:1059–1070. doi:10.1534/genetics.107.075804
- Gram, R., and F. Pirchner. 2009. Relation of genetic distance between cattle breeds and heterosis of resulting crosses. *Anim. Blood Groups Biochem. Genet.* 15:173–180. doi:10.1111/j.1365-2052.1984.tb01114.x
- Groenen, M. A. M. 2016. A decade of pig genome sequencing: a window on pig domestication and evolution. *Genet. Sel. Evol.* 48:23. doi:10.1186/s12711-016-0204-2
- Hayes, B. J., A. J. Chamberlain, S. Maceachern, K. Savin, H. McPartlan, I. MacLeod, L. Sethuraman, and M. E. Goddard. 2009. A genome map of divergent artificial selection between *Bos taurus* dairy cattle and *Bos taurus* beef cattle. *Anim. Genet.* 40:176–184. doi:10.1111/j.1365-2052.2008.01815.x
- Jimenez, J., K. Hughes, G. Alaks, L. Graham, and R. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. *Science* 266:271–273. doi:10.1126/science.7939661
- Lembeye, F., N. López-Villalobos, J. Burke, and S. Davis. 2016. Breed and heterosis effects for milk yield traits at different production levels, lactation number and milking frequencies. *New Zeal. J. Agric. Res.* 59:156–164. doi:10.1080/00288233.2016.1156551
- Leroy, G. 2014. Inbreeding depression in livestock species: review and meta-analysis. *Anim. Genet.* 45:618–628. doi:10.1111/age.12178
- Liang, G. H., C. R. Reddy, and A. D. Dayton. 1972. Heterosis, inbreeding depression, and heritability estimates in a systematic series of grain sorghum genotypes1. *Crop Sci.* 12:409. doi:10.2135/cropsci1972.0011183X001200040003x
- Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* (N. Y.). 45:622. doi:10.2307/2409915
- McDowell, R. E. 1985. Crossbreeding in tropical areas with emphasis on milk, health, and fitness. *J. Dairy Sci.* 68:2418–2435. doi:10.3168/jds.S0022-0302(85)81118-8
- Merilä, J., and B. C. Sheldon. 1999. Genetic architecture of fitness and nonfitness traits: empirical patterns and development of ideas. *Heredity* (Edinb). 83(Pt 2):103–109. doi:10.1046/j.1365-2540.1999.00585.x
- Notter, D. R., B. Scherf, and I. Hoffmann. 2013. Breeding of Animals. In: S. A. Levin, editor. *Encyclopedia of biodiversity*. 2nd ed. Elsevier, New York. p. 636–649.
- Penasa, M., M. De Marchi, R. D. Zotto, G. de Jong, G. Bittante, and M. Cassandro. 2010. Heterosis effects in a black and white dairy cattle population under different production environments. *Livest. Sci.* 131:52–57. doi:10.1016/j.livsci.2010.02.027
- Powers, L. 1944. An expansion of Jones's theory for the explanation of heterosis. *Am. Nat.* 78:275–280. doi:10.1086/281199
- Robinson, T. P., P. K. Thornton, G. Franceschini, R. L. Kruska, F. Chiozza, A. Notenbaert, G. Cecchi, M. Herrero, M. Epprecht, S. Fritz, et al. 2011. Global livestock production systems. Food and Agriculture Organization of the United Nations (FAO) and International Livestock Research Institute (ILRI), Rome, Italy.
- Robinson, T. P., G. R. W. Wint, G. Conchedda, T. P. Van Boeckel, V. Ercoli, E. Palamara, G. Cinardi, L. D'Aiatti, S. I. Hay, and M. Gilbert. 2014. Mapping the global distribution of Livestock. M. Baylis, editor. *PLoS One*. 9:e96084. doi:10.1371/journal.pone.0096084
- Roughsedge, T., R. Thompson, B. Villanueva, and G. Simm. 2001. Synthesis of direct and maternal genetic components of economically important traits from beef breed-cross evaluations. *J. Anim. Sci.* 79:2307–2319. doi:10.2527/2001.7992307x
- Sauvant, D., P. Schmidely, J. J. Daudin, and N. R. St-Pierre. 2008. Meta-analyses of experimental data in animal nutrition. *Animal*. 2:1203–1214. doi:10.1017/S1751731108002280
- Schiermister, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. *J. Anim. Sci.* 93:46–52. doi:10.2527/jas.2014-8493
- Sheridan, A. K. 1981. Crossbreeding and heterosis. *Anim. Breed. Abstr.* 49:131–132.
- Syrstad, O. 1985. Heterosis in *Bos taurus* x *Bos indicus* Crosses. *Livest. Prod. Sci.* 12:299–307. doi:10.1016/0301-6226(85)90130-7
- Walling, C. A., D. H. Nussey, A. Morris, T. H. Clutton-Brock, L. E. Kruuk, and J. M. Pemberton. 2011. Inbreeding depression in red deer calves. *BMC Evol. Biol.* 11:318. doi:10.1186/1471-2148-11-318